

end of the reproductive season may mainly serve to replenish allosperm reserves in the storage organ as no further eggs are produced. In this situation, little sexual conflict may occur between the gender roles. This hypothesis needs testing. However, individuals prevented from remating for a longer period did not differ in female fecundity (number of eggs produced and hatching success of eggs) from those that remated earlier, confirming that one successful copulation per reproductive season is sufficient to fertilize all the eggs produced by an individual (Chen & Baur, 1993).

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On the Adaptive Function of the Love Dart of *Helix aspersa*

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Abstract. The phenomenon of “dart shooting” in land snails of the genus *Helix* remains unexplained from an adaptive viewpoint. Data on the sexual behavior of *Helix aspersa* and *H. pomatia* compiled from previous accounts, supplemented with new observations, do not support the traditional hypotheses that the dart serves reproductive isolation or behavioral stimulation/coordination functions. For example, successful copulation does not depend on dart receipt. An alternative class of explanations for dart shooting is considered: sexual selection. Sexual selection hypotheses for dart function, including certainty of parenthood, male manipulation, and female choice (by both fisherian runaway and indicator mechanisms) are reviewed and compared against the observational evidence. The theory of female choice by handicap/indicator/good genes processes is implemented to propose that dart shooting is a male sexual signal used by females to select sperm from among sperm donors. Male manipulation and female choice are not easily distinguishable as adaptive explanations of dart shooting.

INTRODUCTION

The sexual behaviors exhibited by many hermaphroditic land snails (Gastropoda, Pulmonata, Stylommatophora) are well known for their complexity and vigor. A bizarre feature is the sometimes forceful deployment of calcareous spines and darts, as well as of non-calcareous organs. The gross anatomy of these organs and, in some cases, the behaviors associated with them, have been described for many species (references below). It is therefore surprising that these features have not been better investigated from a behavioral ecological perspective. In fact, empirically supported adaptive explanations for their function are lacking.

This is not to say that zoologists have been uninterested in snail sexual behavior and reproduction. The occurrence and natural history of spine, “dart,” and “stimulator” (sarcobelum) use in land snails were noted even before Ashford’s (1883) monograph describing darts and associated structures in British helicids (references in Kothbauer, 1988). Subsequent descriptions for stylommatophoran pulmonates include: for *Helix*, *Cepaea*, *Theba*, *Tacheocampylaea*, *Eobania*, and *Arianta* (family Helicidae): Meisenheimer (1907, 1912), Szymanski (1913), Taylor (1914), Hofmann (1923), Dorello (1924), Graefe (1962), Herzberg & Herzberg (1962), Petersen (1971), Lund (1971), Lind (1976), Jeppesen (1976), Giusti & Lepri (1980), Chung (1987), Beaumont (1988), Giusti & Andreini (1988), and Adamo & Chase (1988); for *Phenacolinax* (Vitrinidae), *Milax* (Milacidae), *Arion* (Arionidae), *Parma* (Parmacellidae), and *Limax* and *Dero-*

ceras (Limacidae): Adams (1898), Gerhardt (1933, 1935, 1940), Quick (1946), Webb (1950), Langlois (1965), Rymzhanov & Schileyko (1991), and Reise (1995); for *Ventridens* (Zonitidae): Webb (1948); for *Helminthoglypta* (Helminthoglyptidae): Webb (1951, 1952); for *Partula* (Partulidae): Lipton & Murray (1979); for *Gymmarion* (Urocyclidae): Binder (1976); for *Euglandina* (Streptaxidae): Cook (1985); and for *Philomycus* (Philomycidae): Webb (1968) and Tompa (1980). Most of these studies were carried out from a perspective of proximate mechanism rather than ultimate adaptation, if function was considered at all. Nonetheless, several hypotheses have been put forward to provide adaptive explanations for snail precopulatory behaviors, and specifically for dart shooting (Dorello, 1925; Diver, 1940; Goddard, 1962; Lind, 1976; Charnov, 1979; Tompa, 1980, 1984; Chung, 1987; Giusti & Andreini, 1988; Leonard, 1991, 1992; Adamo & Chase, 1990, 1996; Baur, 1998). None has received unambiguous empirical support.

This paper has three main purposes: (1) I first describe the sexual behavior of *Helix aspersa* (Müller, 1774) and *H. pomatia* (Linnaeus, 1758). (2) I then review and comment on some of the published hypotheses purporting to explain dart function in these species. Most of these are not wholly consistent with the observed behavior and biology, whereas others may be plausible but remain untested. (3) Lastly, I apply the hypothesis of female choice based on male sexual signals (Andersson, 1994; Charnov, 1979; Fisher, 1915) as an adaptive explanation for dart shooting in *Helix*: dart shooting is a male sexual signal used by females as the basis upon which to select sperm from among several mates. Females choose the fathers of their offspring based on their perception of their mates’ dart shooting effectiveness. However, whereas Charnov

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(1979) explained female choice based on the dart using the fisherian runaway mechanism, I invoke the concept of indicators for "good genes" ("handicaps," Andersson, 1994; Grafen, 1990a, b; Iwasa et al., 1991; Zahavi, 1975, 1977; Zahavi & Zahavi, 1997). The hypothesis is consistent with the known behavior and reproductive biology, but is as yet untested. Although stylommatophorans are simultaneous reciprocal hermaphrodites, I distinguish "male" and "female" attributes throughout this paper.

METHODS

Helix aspersa individuals were collected in Dublin, Ireland and Berkeley, California, USA and purchased from Blades Biological (collected in County Kent, United Kingdom) in March and April 1996. Additional specimens were collected in Vienna, Austria in September of the same year. Within 1 week of receipt, all snails received a unique number painted onto the shell with white non-toxic paint, and were isolated in individual clear plastic half-liter cups with tight-fitting lids. Cups contained 2–3 cm of sand and potting soil mixture. Throughout the experimental period (May 1996–September 1997) the animal cages were cleaned and the snails showered and fed twice weekly with raw vegetables (lettuce, cucumber, carrot, cabbage); crushed oyster shells were provided *ad libitum*.

A total of 246 sexually mature snails, identified as such by the presence of a reflected shell lip, were subjected to a surgical procedure to check for possession of a dart in the dart sac and for the presence of macroendoparasites of the accessory sexual organs. For surgeries, snails were anesthetized/immobilized with 0.1 ml/g of body weight of 0.01% succinyl choline chloride and 4% MgCl₂ with 0.005% added streptomycin (Chung, 1985). An approx. 0.75 cm incision was made in the right side of the body wall approx. 1 cm behind the genital aperture. The dart sac and digitiform glands were lifted out through the incision with a polished glass probe and examined under low magnification with a dissecting microscope. In 106 out of the 246 snails (43%), the dart sac and digitiform glands (Figures 5, 7, 8) were excised; the remainder of the surgeries were sham manipulations. In all surgeries, two sutures were inserted to facilitate wound healing. Snails usually regained body turgor and mobility within 18 hours. Survivability 1 week following the surgery was 83%; there was no significant difference in survivability between dart sac and digitiform-excised and sham-operated snails.

Sexual encounters of *H. aspersa* were staged by introducing 6–12 showered snails into a 10 L plastic basin. Pairs displaying signs of sexual receptivity were removed to a smaller clear plastic cup where they were continuously and closely observed until they either broke off sexual behavior or achieved successful copulation. The occurrence and timing of all behaviors, including dart

shooting and receipt, were recorded for 156 sexual encounters.

Nineteen *H. pomatia* sexual encounters were observed and recorded in the field on the grounds of the Max Planck Institute for Behavioral Physiology near Starnberg, Germany during the spring and summer of 1997. No dissections were performed on *H. pomatia*.

DART-SHOOTING BEHAVIOR IN *HELIX*

The sexual behavior and reproductive biology of *Helix aspersa* and *H. pomatia* (Helicidae, Helicinae) have been well documented. The account given here of *H. aspersa* and *H. pomatia* matings is similar to those of Meisenheimer (1907), Jeppesen (1976), and Giusti & Lepri (1980); Lind (1976), Chung (1987), and Adamo & Chase (1988) gave more quantitative descriptions. The first and second parts of this section cover the precopulatory and copulatory behaviors of *H. aspersa* and *H. pomatia*, whereas the third part addresses additional matters concerning dart shooting and the biology of *Helix*. Results not attributed to previous works have been derived from my own dissections and observations of sexual encounters.

Sexual Behavior

Upon meeting, two receptive *H. aspersa* raise their heads slightly and engage in bouts of mutual facial caressing, mouth-mouth and mouth-genital pore contact, and biting. These behaviors may be punctuated by interruptions (1–20 min in duration) in which the snails separate and/or circle clockwise about one another. The extensive physical contact during this initial phase ("introductory behavior," Lind, 1976) may allow each snail to gather information via mechanical and/or chemical cues regarding the species, size, health, and/or sexual receptivity of its prospective partner. "Receptivity" is here only loosely defined. A receptive snail attempts to initiate sex with every snail that it contacts; other receptive individuals respond to advances from any initiator, whereas non-receptive snails shun such advances. Although subtle precopulatory mate choice may exist in *Helix* and other helicids, there is no direct evidence for it (but see Fearnley, 1996). For example, Baur (1992) and Baur & Baur (1997) found that matings in *Arianta arbustorum* (Helicidae, Ariantinae) occur randomly with respect to shell size and degree of relatedness, respectively.

Within 1–12 minutes after contact between receptive individuals, the genital pore region (GPR), on the right side of the head, becomes swollen. The genital atrium partly everts, and each snail presses its GPR against that of its partner (Figure 1). The mutual GPR contact alternates with mouth-mouth and mouth-GPR contact, biting, and pauses. *Helix aspersa* pairs maintain a side-to-side posture, and although they may raise their heads slightly, each snail retains substrate contact with nearly the entire



Figures 1–4. Courtship of *Helix aspersa*. Images are from different courtship sequences. For scale, snail shells are approx. 2.7 cm along their longest dimension. Figure 1. Early in courtship; neither snail has shot its dart. The genital pore regions (GPRs) of both snails are swollen and everted (white tissue masses between snails' right tentacles), and each snail presses its GPR against that of its partner. Figure 2. The left snail has just ejected its dart (white pointed object emerging from right side of head). The dart did not strike the partner. Figure 3. Unilateral copulation attempt; the snail on the right has everted its penis. The swollen GPR of its partner (to immediate left of penis) is apparent. Figure 4. Successful mutual copulation. Intromission was achieved approx. 2 min before photo was made. The shot dart of the lower snail can be seen protruding from the recipient.

foot (Adamo & Chase, 1988; Chung, 1987). In contrast, *H. pomatia* partners press the front one-third to one-half of the ventral surfaces of their feet together in a "sole-to-sole" posture, raising their heads in a "frontal upright" position (Meisenheimer, 1907; Lind, 1976).

After a variable length of time (in *H. aspersa*, 5–90 min following initial GPR swelling; personal observation), one partner performs dart shooting by forcibly ejecting its dart from the genital pore (Figure 2). As *Helix aspersa* partners are usually in GPR-GPR contact at the time of dart shooting, the shot dart often hits the recipient in or near the GPR; a well aimed and forcefully expelled dart may penetrate the partner's body wall. If the shooter's GPR is not appressed to the partner upon shooting, the dart may miss the intended recipient or strike it without penetrating.

Most sexual behaviors in *H. pomatia* proceed more slowly than in *H. aspersa*, and the postures differ (Jepesen, 1976; Lind, 1976). Prior to dart shooting, and starting from the sole-to-sole, frontal upright posture, *H. pomatia* lowers its head, usually pressing its GPR against the sole of its partner. Lind (1976) noted that *H. pomatia* appears to perform orientation movements before dart shooting. He observed that these movements do not "lead the atrium (GPR) to a specific goal for the dart," but rather ensure that the shooter's GPR is appressed against the partner such that the dart strikes the latter upon being shot. The location of striking and/or penetrating darts differs between the two species, reflecting the different postures of the partners at the time of dart shooting: in *H. aspersa* most darts (60%, Chung, 1987) hit the recipient in or near its GPR, whereas *H. pomatia* darts usually hit

the sole of the foot (75%, Lind, 1976). However, as the partners are not always aligned exactly as described above during dart shooting, darts are received in both species in the head, mantle, penis, body side wall, and foot. Some shot darts miss the intended recipient entirely (8–10%, Adamo & Chase, 1988; Koene & Chase, 1998a; 12%, personal observation; all data from *H. aspersa*). The response to being shot ranges from no observable reaction to a brief (< 30 sec in *H. aspersa*) recoil away from the stimulus, although in rare cases (< 2% of pairings, Chung, 1987) the encounter may be terminated.

In *H. aspersa*, immediately after the first partner shoots its dart, that snail begins attempting intromission (Figure 3): it presses its swollen GPR against that of the partner and periodically (approx. 1/1–5 min) everts its penis. The snail which has not yet shot its dart appears not to allow unilateral intromission; nor does it commence penis eversions itself. Instead, a variable period elapses during which the first dart-shooter attempts intromission unilaterally while the second snail remains in the “pre-shooting” stage, in which it presses its GPR against its partner without everting its penis (Chung, 1987; Adamo & Chase, 1988; personal observation). Zero to 120 minutes after the first dart-shooting event, the second snail shoots its dart, after which it too commences penis eversions. The sequence and variability of dart shooting and the initiation of intromission attempts are qualitatively similar in *H. pomatia* (Lind 1976; personal observation).

Copulation and Spermatophore Transfer

In *H. aspersa* pairs, near-simultaneity of bilateral intromissions appears to be required for successful copulation, as each snail appears not to allow intromission by its partner unless it also achieves intromission. (This is discussed below in the section “Existing Hypotheses for *Helix* Dart Function, Sexual Selection/Conflict Hypotheses.”) In order to achieve successful mutual intromission, it appears necessary that the interval within which *H. aspersa* partners execute simultaneous penis eversions is 5–6 sec or less (personal observation). In addition to near-simultaneity, successful bilateral intromission appears also to require proper orientation of the partners, such that both penes are properly “aimed.” As a result of the apparent difficulty in accomplishing this feat, the time between the onset of mutual intromission attempts and successful mutual copulation is quite variable, in the range 1–120 min for *H. aspersa*. Partners usually perform multiple penis eversions before achieving mutual copulation; Adamo & Chase (1988) reported a mean of 11 per copulant in *H. aspersa*. Nonetheless, undisturbed pairs that have begun mutual copulation attempts usually succeed (95% of cases in *H. aspersa*, $n = 65$ pairs, personal observation). Once successful mutual intromission occurs, *H. aspersa* copulants become quiescent and assume a stereotypical posture with the tentacles extended but

flaccid (Figure 4). After approx. 15–30 min, the tentacles are fully withdrawn and the snails maintain almost complete quiescence throughout the duration of copulation (Adamo & Chase, 1988; personal observation). Copulation in *H. pomatia* differs, and is described below.

Helix aspersa, *H. pomatia*, and many other helicids do not transfer naked sperm during copulation, but rather package it within a spermatophore (*H. pomatia*, Lind, 1973). In *H. aspersa*, formation of the single spermatophore (per snail) begins in the epiphallus and flagellum within 2 minutes after intromission (Adamo & Chase, 1988). Filling of the spermatophore follows, and the sperm-filled spermatophore enters the penis 2–5 hr after the onset of copulation. Bidirectional spermatophore transfer is completed after approx. 5–6 hr, and copulation lasts 6–8 hr (*H. aspersa*, Adamo & Chase, 1988). Occasionally (8% of pairings, personal observation) partners separate before one or both spermatophores have been completely transferred; 0–5 cm of allospermatophore tail can then be seen dangling from the genital pore. The tail is taken up over the next 1–2 hr, but variable lengths of its tip may break off before uptake (10% of 105 spermatophore transfers, personal observation for *H. aspersa*).

The apparent mutual enforcement of mutual intromission and its resulting near-simultaneity apply also to *H. pomatia*, but other aspects of copulation and spermatophore transfer differ in this species: copulation lasts just 5–10 min, and only the spermatophore head and body are transferred during intromission. Formation and filling of the spermatophore are accomplished in < 5 min (Lind, 1976). Afterward, the penes are withdrawn and the partners remain immobile and in sole-to-sole contact while the allospermatophores are actively taken up by both snails. Spermatophore tails can easily be seen being transferred for several hours following withdrawal of the penes. Each partner (*H. pomatia*) aids spermatophore transfer by generating distally directed muscular waves of contraction of its sole (Lind, 1976; personal observation). Complete uptake requires up to 9 hr (mean 5.5 hr, Lind, 1976), during which the snails remain quiescent.

The spermatophore consists of a head/neck, a body holding the sperm, and a long tail (Meisenheimer, 1907; Lind, 1973; Adamo & Chase, 1988). The spermatophore of *H. aspersa* is 12–15 cm long (Adamo & Chase, 1988), whereas that of *H. pomatia* is 10–12 cm (Lind, 1973). In *H. aspersa* the spermatophore is placed into the receiving snail's bursa diverticulum (Figure 5). *Helix pomatia* lacks a bursa diverticulum, and in this species the spermatophore is accepted instead into the bursa copulatrix. During spermatophore transfer, the spermatozoa remain quiescent, but they become activated and begin to exit the spermatophore through its grooved tail approx. 45 min after copulation (*H. pomatia*, Lind, 1973). Individual sperm are approx. 850 μm long (*H. pomatia*, Thompson, 1973).

Baur et al. (1998) found that the amount of sperm transferred in spermatophores of *A. arbustorum* was uncorre-

lated with the sizes of either donor or the partner, the duration of copulation, the partner's previous mating history (virgin or non-virgin), or the amount of sperm received. Control of sperm transfer amount would be expected if males exercise mate choice or if partners "trade" sperm, i.e., if sperm donation is conditional on sperm receipt.

During and after successful spermatophore transfer, the female reproductive tract generates peristalses that pull the allospermatophore into the bursa diverticulum (*H. aspersa*, Koene & Chase, 1998b) or bursa copulatrix (*H. pomatia*, Lind, 1973). In *H. pomatia* the spermatophore exceeds the receiving bursa copulatrix in length, but despite this length advantage it is caused to "crumple up" by the receiver's peristalsis and is pulled entirely into the tract approx. 6–18 hr after copulation (Lind, 1973). The bursa complex functions not to store transferred allosperm but, by the secretion of digestive enzymes, to break down the spermatophore and destroy the sperm remaining in it. In order to escape digestion and to be stored for possible later fertilization of eggs, spermatozoa must move against the peristalsis to reach the spermatheca (sperm storage organ) at the opposite end of the spermoviduct. Distally directed peristalsis of the spermoviduct further retards the migration of allosperm (Figure 5; Lind, 1973). As the reproductive tract may actively inhibit allosperm from reaching the spermatheca, variation in the strength and/or frequency of peristaltic activity could influence the amounts of transferred sperm which are stored vs. destroyed. Curiously, Chen & Baur (1993) and Locher & Baur (2000) found that 8% and 10%, respectively, of *A. arbustorum* failed to lay fertile eggs following a single successful copulation, and in my own experiments with *H. aspersa*, 21% of twice-mated snails ($n = 29$) failed to lay eggs over a subsequent 2-month period. There are many reasons why snails might not lay fertile eggs after copulating, but one possible reason is that none of the sperm received during those copulations was successfully stored.

The anatomy of the spermatheca indicates that the separate storage and/or retrieval of sperm from different matings is at least a possibility. The spermatheca is composed of three to six blind-ended tubules, the walls of which are muscular and lined with ciliated epithelium (*H. pomatia*, Lind, 1973; *H. aspersa*, Brisson et al., 1977). The spermathecae of the helicine helicids *Eobania vermiculata*, *Tacheocampylaea tacheoides*, *H. aperta*, *H. lucorum*, and *Theba pisana* also consist of "one or more blind sacs" (Giusti & Andreini, 1988). The spermatheca is best studied in *A. arbustorum*, in which allosperm are stored in a spermatheca of similar gross structure (two to nine tubules, Haase & Baur, 1995; Baminger & Haase, 1999; Baminger et al., 2000). It is not yet known if sperm from different matings are stored in separate tubules, but it is clear that individuals can use several tubules for sperm storage (Baminger & Haase, 1999). Further, the intricate musculature, innervation, and ciliation of the spermatheca suggest the capacity to control allosperm movements into

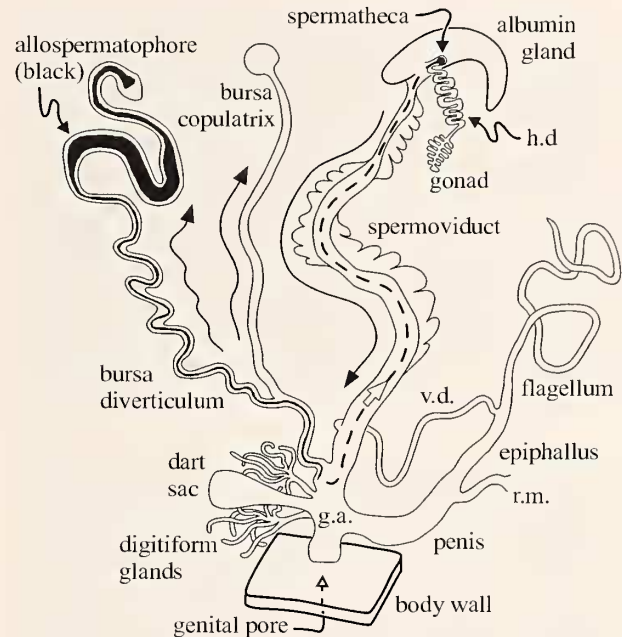


Figure 5. The reproductive organs of *Helix aspersa*, depicted immediately after successful spermatophore receipt. The allospermatophore (black) has been received from the partner into the bursa diverticulum. The thickened portion of the spermatophore is the body, holding the sperm; its tail extends down into the genital atrium. The dotted line (hollow arrowhead) running internally from the genital atrium up the spermoviduct to the spermatheca is the path along which allosperm must traverse in order to be successfully stored. Solid lines with filled arrowheads, drawn outside of the organs, depict reproductive tract peristalses directed against the pathway taken by successfully-stored sperm. A snail's own spermatophore (not shown) is formed and filled in the epiphallus and flagellum and transferred via the everted penis (here shown retracted). g.a., genital atrium; h.d., hermaphroditic duct; r.m., penis retractor muscle; v.d., vas deferens.

and/or out of individual tubules (Bojat et al., 2001). Stored sperm remain viable for at least 1 year in *A. arbustorum* (Baur, 1988) and *Cepaea nemoralis* (Helicidae, Helicinae, Murray, 1964).

Fertilization occurs at oviposition, which can take place from 1 day to many months after copulation (*H. pomatia*, Perrot, 1938 cited by Tompa, 1984). Fertilization occurs in a pouch located at the confluence of the hermaphroditic duct, the spermathecal duct, and the spermoviduct (Figure 5; better illustrated by Lind, 1973). Allosperm are released or transported from the spermatheca to the fertilization pouch, but it is unknown if snails can control the amounts of sperm released from the different spermathecal tubules (see previous paragraph and Bojat et al., 2001). *Helix aspersa* may produce from zero to several clutches following a single mating (Moulin, 1980). The number of matings achieved by wild individuals of *H. aspersa* is unknown, but is likely to be on the order of two to six per year (Baur, 1998). Tischler (1973)

reported that snails of a small population of *H. pomatia* in northern Germany copulated at least two to four times per season, and Lind (1988) found that individuals in his larger Danish population of the same species mated at least five to six times annually. Murray (1964) and Baur (1994) reported that the offspring of wild individuals of *Cepaea nemoralis* and *A. arbustorum*, respectively, were fathered by more than one individual.

The behaviors of some other helicid species may be interpreted similarly. Giusti & Lepri's (1980) and Giusti & Andreini's (1988) behavioral descriptions of *Eobania vermiculata*, *Tacheocampylaea tacheoides*, *H. aperta*, *H. aspersa*, *H. lucorum*, and *Theba pisana* are less quantitative than those of Lind (1976), Chung (1987), and Adamo & Chase (1988), but are qualitatively consistent with the accounts given in those reports and here. The one notable exception is that dart shootings were observed to occur simultaneously in pairs of *E. vermiculata*, *T. tacheoides*, and *T. pisana*; the significance of the differences in simultaneity of dart shootings among species is unknown. In all species studied by Giusti and colleagues, copulation success appeared not to depend on dart receipt.

Dart Characteristics

The following aspects of dart shooting are discussed because of their potential relevance to the dart's adaptive function: (i) the fate of a shot dart, (ii) dart composition and regeneration, (iii) substances transferred by the dart, (iv) common snail parasites, and (v) variability in dart shooting and receipt.

(i) Shot darts do not always strike the partner, and even when they do, they do not always penetrate the body wall. In *H. aspersa*, Chung (1987), Adamo & Chase (1988), and Koene & Chase (1998a) found that a shot dart penetrated the recipient's skin in 67–92% of cases. In the remaining instances the dart either struck the partner but did not penetrate or completely missed. For penetrating darts, the extent of penetration varies from superficial (< 1 mm) to deep (the entire 9 mm length); occasionally a dart is thrust so hard that its tip emerges from the other side of the recipient's body (Figure 4). The duration of penetration varies correspondingly. Deeply penetrating darts often remain lodged in the recipient's skin/body for many minutes to hours, and may even be absorbed (allodart absorption by the recipient occurred in 6–46% of penetrations in *H. aspersa*, Chung, 1987; Adamo & Chase, 1988; Koene & Chase, 1998a). Shallowly penetrating darts usually become dislodged and fall out within seconds or minutes (own data, unpublished). A dart that misses or falls out may simply lie on one of the snails or fall to the substrate.

In *H. aspersa*, of those darts not striking the intended target snail, many are shot so weakly that they are not fully expelled from the shooter's dart sac (Chung, 1987; personal observation). In these and other cases in which



Figure 6. A shot dart (length 9 mm) that missed the intended recipient. The dart base, with adhering digitiform gland mucus, is at bottom.

it fails to lodge in the recipient's skin, the dart may be retracted by the shooter. "Used" and retracted autodarts are held briefly in the dart sac or genital pore, but are later either expelled onto the ground or transferred to the bursa copulatrix/diverticulum (Chung, 1987; J. Koene, personal communication). In any case, a shot dart is not re-used, possibly because upon shooting it becomes physically decoupled from its connection to the "tubercle" within the dart sac. The tubercle, at the base of the dart sac, is the structure upon which the dart forms (Dillaman, 1981). This decoupling is thought to render a dart subsequently unusable (*H. aspersa*, D. Chung, personal communication; *H. pomatia*, Lind, 1973).

(ii) *Helix aspersa* and *H. pomatia* possess only one dart at a time. The dart of *H. aspersa* is approx. 9 mm long (Figures 6, 8) and made of aragonite (CaCO_3) and a protein scaffold (Hunt, 1979; Dillaman, 1981). It bears four blades over most of its length; a cone-shaped base fits over the dart sac's tubercle. After dart shooting, 5–7 days are required for dart regeneration (*H. pomatia*, Jepsen, 1976; *H. aspersa*, Dillaman, 1981; Tompa, 1982). The amount of calcium in a dart (*H. aspersa*: 0.37 ± 0.13 mg, Koene & Chase, 1998a) is approximately equal to that in a single egg, and the mean clutch size for this species is 50–60 eggs (range 20–130, Herzberg & Herzberg, 1962; Koene & Chase, 1998a). The relative amounts of calcium in darts and eggs and the fact that the dart is usually not absorbed by the recipient suggest that the dart calcium does not function as a nuptial gift (Koene & Chase, 1998a), a possibility raised by Charnov (1979) and Leonard (1991). Indeed, J. Koene (unpub-

lished) found that most of the calcium transferred in an absorbed dart is excreted.

(iii) Upon being shot, the dart is liberally coated by a white mucus (Figure 6) secreted by the paired digitiform glands; at least some of the mucus of a well penetrating dart enters the recipient's haemocoel (*H. aspersa*, Adamo & Chase, 1990). The composition of the mucus is unknown. Koene & Chase (1998b) found that *in vitro* application of the mucus induces contractions of the female reproductive tract. These contractions may influence the dart recipient's disposition of the shooter's sperm, an interpretation supported by results reported by Rogers & Chase (2001).

The size and apparent health (based simply on visual inspection) of digitiform glands vary among snails (Ashford, 1883; Taylor, 1914; personal observation). In field-collected adult *H. aspersa* from California, England, and Austria (the last introduced from ex-Yugoslavia, Reischütz, 1978; W. Fischer, personal communication), discolored digitiform glands were found in 2% ($n = 92$), 23% ($n = 92$), and 6% ($n = 62$) of snails, respectively ($n = 246$; this study). Normal glands are white, and discoloration ranges from yellow to brown (Figure 7). Discolored glands contain darker and more viscous mucus than do white, apparently healthy, glands. The discolored-gland condition was found only in non-virgins (personal observation), as determined by the snail's possession of a normal or virgin dart (Chung, 1986b), suggesting that the condition is transmitted venereally. Excluding virgins, the percentages of snails with discolored digitiform glands from the Californian, English, and Austrian populations were 6%, 29%, and 8% respectively (this study). In addition to the digitiform gland discoloration, the glands and/or dart sac bore dark cysts in 2% of the English and 6% of the Austrian snails (this study).

(iv) Wild *H. aspersa* from its native habitat hosts a variety of parasites, some in the reproductive tract. For example, the nematode *Nemhelix bakeri* inhabits the dart sac (Figure 8) and other reproductive organs; venereal transmission occurs via the transferred spermatophore (Morand, 1988) and possibly via dart shooting. Heavy infestations of *N. bakeri* cause decreased fecundity (*H. aspersa*, Morand, 1989). In my *H. aspersa* samples, nematodes were found in 32% of (native) English non-virgins ($n = 22$), but in none of the (introduced) California and Austrian snails. Other parasites of land snail reproductive, digestive, or respiratory systems include the sporozoan *Klossia helicina* (Taylor, 1914), the ciliate *Myxophyllum steenstrupi* (Taylor, 1914), the flagellate *Cryptobia helices* (Lind, 1973), the trematode *Dicrocoelium dendriticum* (Taylor, 1914), the nematode *Rhabditis maupasi* (Brockelman & Jackson, 1974), and the mite *Riccardoella limacum* (Baker, 1970). These parasites affect host fitness (*H. aspersa*, Morand, 1989; Graham et al., 1995) and are often transmitted between snails during sexual encounters (personal observation for the mites on *H. aspersa*; Lind,



Figures 7 and 8. Diseases of the dart sac and digitiform glands. Figure 7. Digitiform glands, one healthy (white) and one diseased (gray; brown in life) from the same snail. Individual tubules were transected to show the consistency of the mucus. The gray mucus is much more viscous than the white mucus, demonstrated by the different extents of diffusion into the saline droplet (white arrows). Tubule widths are approx. 0.75 mm. Figure 8. Nematode parasites of the dart sac. The dart sac (left) was excised from a live snail and the dart (right) was expelled manually. Approx. 30 nematodes (*Nemhelix bakeri*) can be seen in the saline drop; the nematode images appear blurred because the worms were swimming. The white flask-shaped line is the edge of the saline droplet under transillumination. The dart is approx. 8 mm in length.

1973 found that the presence of *Cryptobia* in *H. pomatia* was correlated with previous sexual activity).

Variability in the health of the digitiform glands resulting from disease, parasites, and/or other factors, e.g., senescence, should contribute to the total variation in the amount and/or potential bioactivity of the digitiform gland mucus transferred by dart shooting.

(v) If a sexually active *H. aspersa* possesses a dart, it generally shoots it during precopulatory behavior. That is, for those individuals possessing a fully formed dart, dart shooting is *not* a conditional, i.e., optional behavior (Chung, 1987 and personal communication; personal observation); snails do not "decide" whether or not to shoot

a dart during a particular encounter. (But see Adamo & Chase [1988], who reported that *H. aspersa* failed to shoot a dart, even though individuals had one, in 5% of cases. For at least some reported cases of failures to shoot, it is possible that the dart had in fact been weakly shot and then retracted into the dart sac or genital atrium.) There are, however, two known circumstances in which *H. aspersa* individuals undergo an otherwise normal mating sequence *without* shooting a dart. In both cases, the reason for a snail's failure to shoot is that it lacks a dart. The first instance is that in which a snail mates within approx. 7 days after having shot its dart in a previous encounter. Snails mating in this interval have not yet regenerated a dart, and so do not shoot one. *H. aspersa* individuals are less likely to remate within a 2-day refractory period following copulation (Chung, 1987); *H. pomatia* will remate with either the same or a different individual, without dart shooting, within 3 days of copulating, after which it also experiences an approx. 5-day refractory period (Jeppesen, 1976; Lind, 1976). The second case of non-shooting occurs in virgin snails: in order to produce its first dart, a snail must apparently undergo precopulatory behavior, including the dart-shooting phase (Chung, 1986b). Virgin snails occasionally exhibit conspicuous dart-shooting behavior without expelling a dart: the dart sac is everted, but no dart is present (Adamo & Chase, 1988; personal observation).

In *A. arbustorum* the question whether individuals "decide" to shoot a dart in a given encounter is unresolved. Baminger et al. (2000) dissected snails post-copulation, checking for the presence and locations of shot and un-shot darts. It was found that 60.5% of mating snails held a fully formed dart in the dart sac after copulation, implying that dart shooting occurs in fewer than half of matings, per individual. However, Baminger et al. did not check whether darts found in the dart sac after copulation were detached from the tubercle (*H. Baminger*, personal communication). As discussed above, dart detachment from the tubercle appears in *H. aspersa* and *H. pomatia* to signify an "attempt" to shoot the dart. Except for Baminger et al. (2000), dart shooting has not been studied as well in *A. arbustorum* as it has in *H. aspersa* and *H. pomatia*. The available evidence and observations (e.g., *A. arbustorum*'s relatively larger digitiform glands secrete copious amounts of mucus, which is actively ingested by both partners prior to copulation; B. Baur, personal communication) suggest that dart shooting and mucus production function differently in *A. arbustorum* as opposed to *H. aspersa* and *H. pomatia*.

The above discussions highlight the fact that both dart shooting (occurrence, "force," and "aim") and receipt (occurrence, location, extent, and duration of penetration) are therefore quite variable (Lind, 1976; Chung, 1987; Koene & Chase, 1998a). Moreover, the differences in dart shooting effectiveness and in the quantity and quality of digitiform gland mucus transferred by the dart are likely

to influence the degree of the putative effect(s) on the recipient. Signal variability correlating with signaler viability/quality is a requirement for the indicator/good genes mechanism of female choice, discussed below.

EXISTING HYPOTHESES FOR *HELIX* DART FUNCTION

Although not demonstrated empirically, dart shooting clearly extracts substantial material, energetic, and other costs (e.g., developmental; see the section below "Female Choice Based on the Love Dart, Relevant Aspects of the Reproductive Biology of *Helix*"). What possible benefit could the dart bring which might offset these costs? Existing hypotheses for dart function are of three types (Chung, 1987): reproductive isolation, sexual behavior coordination/stimulation, and sexual selection/conflict.

Reproductive Isolation Hypotheses

Some early workers (Diver, 1940; Webb, 1952) proposed that dart systems evolved and/or currently function to prevent interspecific matings. For many years, until the 1970s, the literature abounded with such explanations for species-specific sexual displays. However, there are several reasons for doubting the validity that this function is the primary one, both for the darts of *Helix*, in particular, and for sexual signals in general (Zahavi & Zahavi, 1997).

First, it is illogical that such a costly feature as dart shooting, performed late in the mating sequence, evolved expressly to prevent interspecific matings. If interspecific copulations result in low-fitness offspring and/or extract other fitness costs, selection would favor unambiguous, early, and relatively cost-free species recognition. In some sympatric *Helix* species, e.g., *H. aspersa* and *H. lucorum*, interspecific mating encounters have never been reported, even though sexually active individuals of both species were kept together for months or years (F. Giusti, personal communication; personal observation). The scarcity of reported helicid interspecific mating attempts suggests that species recognition occurs soon after initial contact between snails.

The hypothesis also predicts that, in order that the dart be used for species discrimination, its associated behavioral, physiological, and/or morphological parameters should be species-specific. The gross similarity of dart use *among* species and the wide variation in dart-shooting parameters *within* species are contrary to the species-discrimination hypothesis. Perhaps the species-specificity of dart shooting lies in the morphology of the dart, or in the composition of the dart mucus? Dart morphologies differ among species (Tompa, 1980), but it is doubtful that snails can "perceive" the shape of received darts, especially given the variability in dart shooting/receipt. Regarding the possibility that the dart mucus is species-specific, the only relevant result is Chung's (1986a) finding

that the helicine helcid *Cepaea nemoralis* exhibited GPR swelling and eversion when injected with *H. aspersa* mucus. The *C. nemoralis* response was qualitatively identical to *H. aspersa*'s response to injection of *H. aspersa* digitiform gland extract. It is therefore unlikely that the digitiform gland mucus acts as a species recognition cue.

Third, the hypothesis predicts that interspecific mating encounters should proceed readily up to the point of dart shooting, immediately after which the pair should break off their interaction. Reports of interspecific sexual encounters in helicids are rare, so it is difficult to find evidence either supporting or refuting this point. Beaumont (1988) reported that *C. nemoralis* and *C. hortensis* engaged in interspecific pairings in dense mixed-species experiments. The interactions were not observed carefully enough, however, to determine whether dart shooting influenced copulations. Petersen (1971) reported a single case of interspecific sexual behavior in which both partners (*C. nemoralis* and *C. hortensis*) passed through dart shooting. Only the *C. hortensis* shot a dart, but this did not strike the *C. nemoralis*; this latter individual exhibited dart-shooting behavior, but no dart was observed. Both snails attempted intromission but the pair failed to copulate. In this well described interspecific mating attempt, the failure to copulate appeared to result not from receiving the incorrect dart, but rather from incompatible copulation behavior. The two partners did not terminate their interaction at the critical stage of dart shooting. Finally, Webb (1951) observed an instance of courtship between two species of *Helminthoglypta* (Helminthoglyptidae). The individual of the larger species shot a dart into the smaller partner, which was gravely injured by the dart receipt. The courtship did not proceed, and the smaller, darted individual died 4 days later. The seriousness of the injury caused by the dart in this case renders Webb's observation difficult to interpret with regard to the dart-as-reproductive-isolation-mechanism hypothesis. Tompa (1980) reported that there are no other recorded observations suggesting that potential interspecific matings are inhibited by the dart.

The logic and evidence reviewed above indicate that the dart-as-reproductive-isolation-mechanism hypothesis should not be considered as a viable adaptive explanation of dart shooting.

Sexual Behavior Stimulation/Coordination Hypotheses

The second hypothesis proposes that dart shooting stimulates the recipient sexually, facilitating temporal coordination between the partners and thereby increasing the likelihood that they achieve copulation. For many years, partner stimulation and/or coordination was a primary explanation for the function of precopulatory/courtship behavior in general (Bastock, 1967). Evidence specific to *Helix* consists of observations of the immediate

effects of dart shooting and receipt, or of injection of digitiform gland mucus, on sexually active snails.

A common idea has been that the digitiform gland mucus transferred by the dart contains a bioactive substance that stimulates the recipient. Dorello (1925) injected digitiform gland mucus into *H. aspersa* and found that the treatment elicited body wall musculature contractions and stimulated the nervous and reproductive systems. Goddard (1962) found in *H. aspersa* that the injury to snails caused by dissection induced activity of the penis, and proposed that dart penetration would have the same effect. He reported no effect of injection of digitiform gland mucus on the penis, concluding that the penis activity was induced by the physical trauma of dart receipt. Injection of digitiform gland extract by Börnchen (1967) in *H. pomatia* increased the frequency and amplitude of heart contractions. Chung's (1986a) injection of *H. aspersa* with digitiform gland extract caused eversions of the genital atrium and/or penis, in agreement with Dorello (1925). His conclusion was that "the dart may be used for traumatic inoculation of the mating partner with a contact pheromone that enhances sexual receptivity."

Adamo & Chase (1988) compared the durations of sexual stages in dart recipients and non-recipients of *H. aspersa*. The only difference found was the time between the first and second dart-shooting events: if the first dart hit and penetrated the recipient, the time to the second dart-shooting was significantly reduced by a mean of 26 min. No correlations were found between dart shooting/receipt and either the interval from the second dart shooting to successful copulation or the duration of copulation. The mean duration of the entire mating sequence was approx 490 min; the 26 min reduction thus represents a 5.5% time savings. Adamo & Chase (1990) subsequently showed, using dart sac- and/or digitiform gland-extirpated snails, that the decrease in courtship time was caused by the digitiform gland mucus, not by dart receipt alone: snail pairs that shot "dry" darts experienced matings that lasted as long as dartless pairings. Injection of digitiform gland extract into sexually active snails similarly produced a small but significant decrease in time-to-copulation, but only if the injection occurred when the snail was at an intermediate stage of sexual arousal (Adamo & Chase, 1990). Digitiform gland extract injection also inhibited locomotion and induced a temporary increase in the level of GPR eversion. Adamo & Chase (1990) concluded that the dart mucus contains a pheromone that reduces the time that the partners are in different, non-complementary stages. They speculated, but did not demonstrate, that this effect raises the likelihood that pairs copulate successfully.

The hypothesis that dart shooting functions to stimulate mutual sexual behavior, thereby increasing the probability of successful copulation, is contradicted in two thorough studies. Lind (1976) tested in *H. pomatia* whether dart receipt affected the partners' level of sexual activity, du-

ration of precopulatory behavior, and probability of successful copulation. By switching partners between two snail pairs (putting the first dart shooters together) he created pairs in which neither partner received a dart. Snails manipulated in this way mated normally. He found that such pairings resulted in significantly *shorter*, not longer, times-to-copulation; precopulatory behavior in pairs in which neither snail, one snail, and both snails received a dart lasted on average 3.0, 4.2, and 5.2 hr, respectively. He further reported that the post-dart-receipt behavior of a snail depended chiefly on that snail's activity level just prior to being shot: if the recipient was active before being shot, it remained active; if passive, it remained passive. Of those snails showing a change in activity upon dart receipt, twice as many became *less* active than more so. These observations led Lind (1976) to conclude that no facilitative effect of the dart on subsequent behavior of the recipient exists.

Lind's (1976) analysis was largely descriptive, although he did not refrain from commenting on the apparent non-adaptiveness of dart shooting. In contrast, Chung's (1987) study of sexual behavior in *H. aspersa* was undertaken deliberately "in order to document in detail the courtship of this snail and to determine whether dart receipt stimulates courtship or has another function." Chung (1987) carefully assayed the behavior of paired snails that either received a dart or not. As measures of sexual arousal he used the biting rate, the fraction of time spent out of mutual genital contact, and the rate of attempted copulation. He found no significant differences in the first two parameters between dart-receiving and non-dart-receiving snails. Additionally, in snails receiving a dart there were no significant differences before and after dart receipt in the biting rate or the fraction of time spent out of genital contact. Snails receiving a dart had significantly *lower*, not higher, rates of attempted copulation (the third parameter, above) than those not receiving a dart. In contrast to Adamo & Chase (1988, 1990), Chung (1987) did not find that the time between the first and second dart-shooting events was shorter if the first dart penetrated the recipient.

What can be concluded regarding the hypothesis that the dart functions to stimulate and/or coordinate snail sexual behaviors? That dart receipt has no demonstrable effect on the probability of copulation rules out a role for the dart in the overt stimulation of sexual behavior. (However, the effects of dart and/or digitiform gland mucus receipt may not be limited to those observable externally. As mentioned, Koene & Chase [1998b] found that digitiform gland mucus induced contractions of the female reproductive tract. The potential adaptive consequences of such "cryptic" effects of dart receipt are discussed below.) Coordination of sexual behavior by dart shooting may be admitted only if a perverse concept of coordination is applied: at the onset of precopulatory behavior, before the first dart-shooting event, the partners' behav-

iors are well synchronized; they become asynchronous and non-complementary upon the first dart shooting; and they are resynchronized only after the second dart shooting (Lind, 1976). Lind's (1976) and Chung's (1987) conclusions regarding the dart's effect in *H. pomatia* and *H. aspersa*, respectively, were that the dart does not function to synchronize or coordinate sexual behavior.

The observations of Giusti & Lepri (1980) and Giusti & Andreini (1988) of matings in *H. lucorum*, *H. aperta*, *Theba pisana*, *Tacheocampylaea tacheoides*, and *Eobania vermiculata* also fail to support the hypothesis that the dart coordinates/stimulates sexual behavior. These authors reported that copulation proceeded normally in the absence of dart receipt, although they did not quantify the times-to-copulation of dart-shooting vs. non-dart-shooting pairs. Giusti & Andreini (1988) hypothesized that dart shooting functions to test the partner's sexual receptivity or motivation. Assuming that biting and dart receipt represent adverse stimuli, Giusti and collaborators reasoned that only highly motivated snails proceed to copulate in the face of such noxious stimuli. Unmotivated snails would be identified and filtered out by dart shooting, leaving sexually motivated snails to concentrate their efforts on like individuals. There is no evidence to support this hypothesis. Once two snails pass through introductory behavior to the dart-shooting stage, the probability that they will proceed to copulation is quite high (approx. 95% in *H. aspersa*; personal observation), and does not depend on dart shooting/receipt. Also at odds with Giusti's hypothesis is the fact that, by shooting a dart at a given partner, the shooting snail forgoes the opportunity similarly to "test" other prospective partners for at least 7 days, the time required to manufacture a new dart. Other tactics to assess partner motivation, e.g., the extensive facial, oral, and genital contact occurring prior to dart shooting, would be far less costly to the snail doing the testing.

The evidence that dart shooting functions to stimulate the partner's sexual activity and/or to coordinate the snails' behaviors is at best equivocal. That dart shooting precedes copulation need not mean that its function is to facilitate the latter act.

Sexual Conflict/Selection Hypotheses

Explanations of a different sort propose that the dart is an adaptation to resolve sexual conflict. These hypotheses generally assume that one of the sexual roles (male or female) is "preferred" over the other. That is, the biological constraints of a hermaphroditic species are such that the cost/benefit ratio of reproduction via one sexual mode is more favorable than that via the other, at least under certain conditions or at specific life history stages. Individuals will be selected to prefer to mate in the role offering the better cost/benefit tradeoff. If the same mode is preferred by all or most individuals, a conflict of in-

terest occurs between potential partners over the assumption of sexual roles (Charnov, 1979; Leonard, 1991, 1992). Conflicts of interest may arise between partners regarding the fates of gametes and zygotes and/or the amounts and kinds of resources invested in offspring by each partner. As paternal care is absent in pulmonates, the only conflicts of interest possible in this group are those regarding the extent of maternal provisioning and the fates of gametes.

Here I discuss two sexual conflict hypotheses as applied to animal hermaphroditic mating systems: Bateman's principle and certainty of parenthood. Bateman's (1948) principle states that the main factor constraining paternal fecundity is the male's ability to gain access to females and/or their eggs, whereas the corresponding limitation on maternal fecundity is the female's ability to convert resources into offspring. These constraints give rise to the situation in which potential individual fecundity via male function is greater than that via female function. Applied to hermaphrodites, Bateman's principle implies that individual hermaphrodites should prefer to reproduce via the male mode. Extending Bateman's logic, Charnov (1979) reasoned that simultaneous hermaphrodites pursue matings not so much to receive allosperm for fertilization (female function), but rather to obtain opportunities to inseminate partners (male function).

Chung (1987) first proposed that the *H. aspersa* dart serves to resolve the sexual conflict of interest between mating partners. Starting from the assumption that the male role is preferred, he hypothesized that male-acting snails shoot darts to coerce partners into accepting their (the shooter's) sperm and using it for fertilization. As one possible mode of dart-mediated partner coercion, Chung (1987) speculated that receipt of the dart and/or digitiform gland mucus might induce oviposition. However, Koene & Chase (1998a) reported no difference in oviposition rates or amounts between dart recipients and non-recipients (*H. aspersa*), and Baur & Baur (1992) found that precopulatory behavior, including dart shooting, did not increase oviposition in *A. arbustorum*. Other possible effects of dart receipt proposed by Chung (1987) are that the dart/mucus may serve to potentiate transferred sperm, inhibit sperm digestion, induce the displacement of previously stored sperm, suppress subsequent mating activity, or inhibit the storage of subsequently received sperm. He further speculated that "the dart may have evolved . . . in a kind of evolutionary escalation that allowed the evolution of increasingly larger or more effective darts to force the partner to act as a female" (Chung, 1987). Chung failed to consider, however, any possible evolutionary response by dart receivers to the coercive effects of the dart/mucus: if dart receipt entails a reproductive fitness cost, selection should favor adaptations to counter its effects.

Adamo & Chase (1996) restated Chung's (1987) hypothesis more strongly by proposing that dart shooters

manipulate their partners' reproductive physiology for their own (the shooter's) benefit. Adamo & Chase (1996) did not explicitly specify the fitness effect of receiving a shot dart, but by using the term "manipulate" they imply that the fitness of dart recipients is decreased. The same objection raised above regarding the evolution of resistance to the dart effect is applicable here, although Adamo & Chase (1996) speculated that the active ingredient in the dart mucus could be identical to a compound used by snails to control their own reproductive functions. If so, then any response evolved to combat the dart mucus effect might also interfere with a snail's ability to control its own female reproductive processes.

More recently, Koene & Chase (1998b) showed that the *in vitro* application of digitiform gland mucus to *H. aspersa* preparations induced muscular contractions and reconfigurations of the female genital tract. Specifically, the mucus acted to constrict the entrance to the bursa copulatrix (the sperm digestive organ) and to elicit peristalsis in the bursa diverticulum to pull in the received spermatophore. Both of these influences probably affect the fate of received sperm. Koene & Chase (1998b) interpreted their result in accordance with Chung's (1987) and Adamo & Chase's (1996) explanation for the dart: dart shooting is an adaptation by which males manipulate females to maximize their own (male) reproductive success. Koene & Chase (1998b) concluded, however, that the reason why males attempt to manipulate females via the dart derives from sperm competition. That is, the evolutionary rationale for dart shooting and for analogous male manipulative efforts is that they allow males to compete successfully against rival males.

Another concept relevant to sexual conflict and preferred sexual roles is "certainty of parenthood" (Leonard, 1991, 1992). In most mating systems, the certainties of parenthood of the female and male are likely to be unequal; the sex controlling fertilization has greater certainty that the investment committed will result in offspring. For example, in promiscuously mating species with internal fertilization, a mated female can ensure that all of the eggs she produces will both be fertilized and be her own, whereas a male is less certain that his mate's offspring will be fathered by him. Leonard (1992) proposed that the female role would be preferred in land snails due to that sex's greater certainty of parenthood. She hypothesized that the dart functions as an honest signal that the shooter will perform the less-preferred male sexual role (to donate sperm without guarantee of paternity) in order thereby to have the opportunity to reproduce in the preferred female role (to receive sperm and be guaranteed of maternity). Several predictions pertinent to the mating system of *H. aspersa* follow from the hypothesis, some of which were addressed by Adamo & Chase (1996).

The first prediction of Leonard's (1992) hypothesis as applied to *H. aspersa* is that non-dart-shooting individuals should be unwilling or unable to perform the male

role, i.e., to donate sperm to their partners. Contrary to this prediction, Adamo & Chase (1988) reported that all snails achieving successful intromission transferred a spermatophore ($n = 70$), whether they had shot a dart or not. Similarly, Baur et al. (1998) reported all copulants (*A. arbustorum*, $n = 92$) transferred spermatophores, 91 of which (99%) contained sperm.

Another prediction (Leonard, 1992) is that non-dart-shooting partners are unattractive as female mates because a snail's non-receipt of a dart might imply that its partner has mated within the last week (and thus recently received allosperm) or is a virgin. The first difficulty with this prediction is that it is not obvious why virgin snails would make poor female mates, as there is no evidence that reproductive abilities are affected by prior experience. Virgin snails may in fact be *more* attractive mates, as they lack previously stored allosperm and are less likely to carry venereally transmitted parasites. Second, non-receipt of a dart need not mean that the partner did not shoot a dart; the partner could have shot but missed. Dart non-receipt is thus not a reliable indicator of a partner's recent mating history. Further, snails which have recently received sperm may nonetheless be desirable as female mates, as subsequently received sperm can still be stored and used for fertilization. Baur (1994) found in *A. arbustorum* that the second (last) male to mate sired a mean of 32% of offspring; the range was 0–100%. Finally, if non-dart-shooting partners make poor female mates, one would expect snails not to copulate unless a dart had been received. This prediction is refuted by Lind (1976), Giusti & Lepri (1980), and Chung (1987).

A third prediction (Leonard, 1992) is that snails should refuse to intromit and/or to transfer sperm unless the partner reciprocates. That is, snails should decline to copulate as males only. It is true that unilateral intromissions are generally disallowed; the question is whether these are prevented from the male or female side. Rarely, one of a pair of snails succeeds briefly in achieving unilateral intromission. In these cases, both Giusti & Lepri (1980) and Chung (1987) reported that the intromitted snail appeared to expel its partner's unilaterally intromitted penis. Chung (1987) observed in these cases that the intromitting (male-acting) snail assumed the typical copulatory, i.e., quiescent, posture. The female-acting snail, in contrast, attempted actively to pull away and bite the partner's penis until it was withdrawn. It thus appears that a snail will consent to unilateral intromission only if it is the "intromitter," but will not allow unilateral intromission if it is the "intromittee." This is exactly the opposite of what Leonard's (1992) hypothesis predicts.

A theoretical deficiency of Leonard's hypothesis is that there appears to be no functional or mechanistic reason why dart shooting should serve to signal reliably that a snail will perform the less-preferred male role of delivering sperm. What prevents a snail from shooting a dart and then not transferring sperm?

In sum, the hypothesis (Leonard, 1992) that dart shooting in *Helix* is an adaptation to resolve the sexual conflict between snail partners preferring to mate as females is logically tenuous, and its empirical predictions appear to be refuted by the available evidence (Adamo & Chase, 1996).

FEMALE CHOICE BASED ON THE LOVE DART

If the critiques given above are deemed acceptable, then only two hypotheses for the adaptive, ultimate function of dart shooting remain viable. (Proximally, dart receipt probably influences allosperm storage and digestion; Koene & Chase, 1998b.) One is that dart shooting is a male manipulative adaptation by which males compete with rival males by influencing their partners' usage of allosperm (Adamo & Chase, 1996). The other is that the dart is a male sexual signal used by females to select sperm received from different mates, i.e., females choose the fathers of their offspring based on their mates' relative dart shooting abilities (Charnov, 1979). The two hypotheses need not be mutually exclusive (Leonard, 1991). In this section I first review the logic of male manipulation and subsequently further develop the female choice hypothesis for dart function. I conclude by discussing known aspects of snail biology, as well as further experimental work, that may provide clues regarding the relative validity of these two hypotheses.

Male Manipulation

Chung (1987), Adamo & Chase (1996), and Koene & Chase (1998b) hypothesized that *H. aspersa* individuals shoot darts in order to manipulate their partners into preferentially using their sperm for fertilization. This sort of manipulation is adaptive only if females mate promiscuously, and is therefore fundamentally a manifestation of male-male competition over access to females' eggs. If females were to mate with only a single male, then the reproductive interests of the two partners would be identical—both partners would achieve maximum reproductive fitness via the female's use of the male's sperm to fertilize all of her eggs—and the reproductive interests of the male would not be served by his attempting further to alter the female's use of his sperm. It is only when females receive sperm from more than one male that the interests of male and female partners come into conflict; one consequence of this is that males would then be selected to compete vicariously with rival males within the arena of the female (Eberhard, 1996). Selection on males to outcompete rivals for fertilization opportunities leads to the evolution of a class of manipulative strategies for biasing female reproduction, e.g., mate guarding, removing rival sperm, inducing oviposition, and influencing females' sperm handling (Andersson, 1994). In *H. aspersa*, the effects of the dart mucus on the female reproductive tract (Koene & Chase, 1998b), leading to the preferential

storage and/or use of transferred sperm, may represent such an apparently manipulative strategy derived from male-male competition.

Although the aim of male manipulative efforts is not explicitly to harm females, but rather to outcompete rival males, the influences listed above are not necessarily in the health and/or fitness interests of females. For example, copulating male *Drosophila* transfer to females seminal fluid compounds that incapacitate previously stored sperm, thereby providing the last-mating male with a sperm competition advantage (Harshman & Prout, 1994). The effects of these compounds on females are not entirely benign; females receiving more seminal fluid products suffered an increased death rate (Chapman et al., 1995). Chapman et al. (1998) found that mating reduces survival in females of 10 of 29 insect species from five of nine families. While the data do not represent an overwhelming trend, the positive cases indicate that receiving courtship and/or copulation exacts physiological costs, at least in some species. Further, Chapman et al.'s (1998) own results on the fly *Ceratitis capitata* point to independent survival costs derived from copulation (including the receipt of courtship) and from egg production. That is, the simple act of engaging in copulation and in-copula courtship comprises a cost of mating distinct from that of egg production. Additional examples of male strategies to influence female reproduction, and their effects on female physiology and fitness, are given by Eberhard (1996) and specifically in hermaphrodites in Michiels (1998).

It is important to distinguish between health/survival costs and total lifetime fitness costs; demonstration of the former does not automatically implicate the latter. In *Drosophila*, in which physiological costs of mating to females have been observed (Fowler & Partridge, 1989; Chapman et al., 1995; Chapman & Partridge, 1996), females allowed to choose their mates produced offspring with greater viability than did females denied a choice of mates (Partridge, 1980). Thus, even though females' receipt of courtship and mating can damage their health, they can nonetheless reap a fitness benefit by using courtship to assess and choose mates. This latter result was confirmed in *Drosophila* by Hoikkala et al. (1998), who additionally showed that specific components of the male sexual signal correlate with viability. Results demonstrating female benefits of choice based on receipt of male courtship have also been reported in other species (Welch et al., 1998; Alatalo et al., 1998). (Studies giving examples in which no significant indirect benefits appear to be derived from mate choice also exist; Alatalo et al., 1998.) The coexistence of these apparently paradoxical consequences of female receipt and assessment of male courtship, i.e., that they exact proximate costs but bring ultimate benefits to females, probably represents a general phenomenon.

Can male manipulation alone, arising from male-male competition, explain courtship behavior? A potential dis-

inction between male manipulation and female choice hypotheses of dart function is that females should reap a net fitness benefit if they are using the information contained in the courtship signal as a basis for mate choice, whereas they are unlikely to benefit if they are the objects of manipulation only. Further, if male manipulation has detrimental health effects on females, as in *Drosophila* (Partridge, 1980) and *Ceratitis* (Chapman et al., 1998), but females nonetheless gain net fitness from receiving and utilizing sexual signals, then the evolution of courtship must be driven at least in part by female choice.

Female Choice in *Helix*: Runaway vs. Indicator Mechanisms

Male manipulation does not consider the potential adaptive use by females of information contained in male courtship behaviors. The use of this information to inform mate choice may be selected if it allows choosy individuals to bear offspring in higher number and/or of higher quality. In many taxa, including *Helix*, males provide no direct benefits to their mates; female choice in these species is therefore unlikely to offer benefits via augmented fecundity. Instead, in species in which males provide nothing but sperm, female choice may bring indirect (genetic) benefits only.

Charnov (1979) hypothesized that the dart is a male sexual signal coevolved with a female preference for dart shooting via a fisherian runaway process. In runaway, the genes for the male signal trait and for the female preference become linked through assortative mating between males expressing the signal, and females expressing the preference for it (Andersson, 1994). To get started, the process requires that females initially prefer males bearing a particular perceivable trait. The specific origin of the pre-existing female preference is irrelevant; for example, it could be inherent in the species' sensory system (Ryan, 1990). Although the initial source need not be specified in order to propose subsequent trait-preference coevolution by runaway, Charnov (1979) nevertheless gave two hypotheses to explain why females might initially have preferred ancestral dart shooters: the dart (or its forebear) was a nuptial gift of calcium, and/or it demonstrated an increased ability to metabolize that resource.

Once a runaway process is underway, it no longer relies upon whatever correlation may have formerly existed between the male signal trait and other traits; the genetic linkage between the male signal trait and the female preference is alone sufficient to maintain their subsequent coevolution. The signal trait is therefore likely to come to be arbitrary with respect to other male characters. Charnov clearly cited the runaway process itself as the mechanism by which dart shooting evolved and is maintained; the hypothesized correlations between the dart and other male qualities were simply his guesses as to how the process began (Charnov, 1979:2483): "One wonders if the

love darts of some snails are the result of such a (runaway) process."

Twenty years passed before experimental studies were undertaken to test Charnov's hypothesis regarding dart-based female choice in snails. Koene & Chase (1998a) refuted the idea that the dart is a nuptial gift of calcium: the dart contains too little of that element relative to the amount in a clutch of eggs, and it is only rarely absorbed by the recipient. Further, J. Koene (unpublished) found that the calcium in absorbed allodarts is excreted. The hypothesis given here for the dart's adaptive function picks up on Charnov's second notion, that dart shooting is a "demonstration . . . of increased ability" (Charnov, 1979:2483). Charnov did not develop this idea into a distinct hypothesis for dart shooting nor as an explanation for the evolution of sexual signals in general. (Subsequent authors have done the latter; Andersson, 1994.) At the time, Zahavi's (1975, 1977) "handicap principle," also known as the "indicator" and "good genes" hypothesis when applied to sexual selection, had just been published as an explanation for the evolution of female preferences and male sexual signals. As individual reproductive fitness is influenced in part by offspring quality, there is selective pressure on individuals to maximize the genetic quality of their offspring via mate choice. Applied to sexual selection, the handicap principle states that honest signaling systems evolve in response to selection for the identification of high genetic quality mates: as a result of pressure on individuals to secure mates with good genes, preferences evolve for traits that correlate with, and therefore indicate, the genetic quality of potential mates. The ideal preferred trait is that whose magnitude varies perceivably and reliably with mate quality; these preferred indicator traits can coevolve with the preference to become sexual signals. (The handicap principle may be applied to other communication systems, such as between predators and prey. I use "indicator," as have others [e.g., Andersson, 1994], to refer to a signaling mechanism in which a "handicap" trait conveys information about the genetic quality of potential mates.)

Population geneticists were slow to accept the operation of the indicator mechanism (e.g., Bell, 1978), and perhaps Charnov (1979) considered it to be an unlikely explanation for dart shooting. Regardless, the runaway and indicator hypotheses are now thought to be the best explanations for the evolution of preferences for sexual signals (Pomiankowski, 1988; Andersson, 1994; Andersson & Iwasa, 1996).

The hypothesis presented here is that dart shooting in *Helix* evolved as a male sexual signal used by females as an indicator of mate viability. Females choose the fathers of their offspring by selecting which received allosperm to use for fertilization of their eggs based on their assessment of their mates' sexual signal—dart shooting effectiveness. Charnov (1979) explained the dart by the runaway process; I invoke the indicator mechanism. A

crucial consequence of female choice by the indicator mechanism, as opposed to runaway, is that the positive correlation between magnitude of expression of the signal trait and mate quality provided by the indicator mechanism allows females to produce offspring of above-average viability. If population viability is sub-maximal and if viability is heritable, females gain a distinct fitness benefit via the indicator mechanism. (An additional consequence, relevant to species selection, is that sexual selection by female choice by the indicator mechanism potentially increases population viability above the level achieved by natural selection alone.) In contrast, in runaway the relationship between the signal trait and mate quality is arbitrary, and so, on its own, sexual selection by the runaway process does not generate increased offspring fitness, relative to natural selection alone.

Gaining indirect fitness benefits via female choice appears simple in principle, but a practical difficulty arises for females: how to identify high-viability mates? Females will generally not be able to evaluate mate viability directly, casually. Instead, they must "search" for a perceivable male trait whose magnitude correlates with viability. ("Perception" does not require consciousness, nor even nervous system involvement.) Preferences for specific traits may arise as a consequence of sensory biases (Ryan, 1990) or other attributes of a species's biology. Of the many possible traits expressed by males and preferred by females, the expression of one or some of these traits may be correlated with viability such that high-viability males tend to express the trait better. Other male traits will bear no such correlation, or a weaker one, with viability. Females perceiving and preferring the male trait with the tightest correlation with male viability will consequently mate with that non-random sample of males having highest mean viability. If viability is sufficiently heritable and the fitness benefit to females outweighs the cost of choosing (Andersson, 1994), both female preference and male trait—sexual signal—will be selected.

Which male traits correlate best with mate viability, eventually evolving into male sexual signals? The unifying feature of such traits, regardless of a given species's biological constraints, is costliness. Precisely because signals are costly, higher-viability males can better support them than can lower-viability males. Critically, the proportional cost that a high-viability male supports by bearing a given signal is less than that borne by a low-viability male bearing the same-magnitude signal (Grafen, 1990a, b; Getty, 1998). The costliness of sexual signaling therefore ensures the correlation between a male's viability and his ability to signal. Such signals are thus *non-arbitrary*, in that they have evolved so as to be *indicators* of the bearer's viability (Zahavi & Zahavi, 1997).

Relevant Aspects of the Reproductive Biology of *Helix*

Male manipulation and female choice need not be mutually exclusive and can in fact be seen as two sides of

the same process. According to Eberhard (1998), we can think of females as setting the rules of the game and males as the more active players. Likewise, if female choice occurs in a given species, both the runaway and indicator/good genes mechanisms may be operating. Here I review some aspects of the biology of *Helix* which may support the female choice perspective of the evolution of the adaptive function of dart shooting.

(i) The gross anatomical and behavioral characteristics of *Helix* and some other helicids provide ample opportunities for mate choice. Courtship and promiscuity allow both the assessment of multiple mates and the receipt of sperm from those mates. The indiscriminate acceptance of sperm from all partners might be taken as evidence against mate choice. However, *Helix* and some other helicids have evolved elaborate anatomical adaptations that allow both the selective digestion and long-term storage of allosperm (Tompa, 1984; Baur, 1998). Of the sperm received from a given single copulation, only a very small portion is stored (Lind, 1973). It is unlikely that the quantities of sperm stored from each copulation are equal, and Koene & Chase's (1998b) finding that the dart mucus affects contractions of the female reproductive tract suggests that the amount of allosperm stored depends on dart receipt, which in turn depends on the partner's dart shooting ability. If an individual's dart shooting ability correlates with its viability, then female choice in *Helix* may be manifested by a snail's ability to control the amount of allosperm stored from each copulation based on its perception of its mate's dart shooting. This perception need not be "conscious," as the regulation of sperm storage by dart/mucus receipt could be mediated by a simple chemosensory/endocrine pathway. Alternatively, individuals may exercise female choice by selecting which stored sperm (of those received from different mates) are used for fertilization of eggs. Such a selective sperm retrieval mechanism would require both the separate storage of sperm from different mates and a memory of whose sperm is in which spermathecal sac; there is no evidence for either of these phenomena. By whatever mechanism, mate choice by sperm selection in *Helix* and other species with similar mating systems (Michiels, 1998) may occur cryptically after copulation but be based on information received during courtship before, during, and/or after copulation (Eberhard, 1996, 1998).

(ii) Can individual snails reap indirect benefits from female choice of mates? The resolution of this issue relies largely on estimates of genetic variation and heritability of viability traits. Potential sources of genetic variation include parasite-host coevolution (Hamilton & Zuk, 1982), immigration of individuals adapted to different local conditions (Slatkin, 1978), and mutation (Kondrashov, 1988). Although all of these factors likely maintain the genetic variance and heritability of viability traits above zero, the question remains whether the magnitudes of these two parameters in natural populations are sufficient

to make mate choice worthwhile. Multiple studies (references in Dupont-Nivet et al., 1997) on genetic variation and heritability in *H. aspersa* indicate that, for example, shell size is heritable (shell dimension heritabilities of 0.2–0.8 are cited). Dupont-Nivet et al. (1997) found heritabilities of approx. 0.4 for both shell size and body weight, two traits that likely affect viability. What is lacking is a rigorous population genetic analysis determining whether the heritability values found empirically are in fact sufficient to allow mate choice to be adaptive. In addition to the measured heritabilities, a proper analysis would require extensive data regarding the species's life history, mating system, mutation rates, parasites, etc. In the absence of such a study, it nevertheless seems reasonable to propose that snails do indeed have something to gain from mate choice.

(iii) Relevant to the heritability issue is the fact that native populations of *Helix* and some other helicids harbor a multitude of parasites. "Arms races" in which evolving parasite adaptations continuously exert pressure selecting for host counteradaptations are likely to boost genetic variation and heritability of viability traits (Hamilton & Zuk, 1982). Of additional interest is the fact that many parasites of helicids inhabit the host's reproductive tract and/or dart-associated organs themselves; parasite transfer is venereal, and parasitism may directly affect a snail's ability to generate the sexual signal.

(iv) Both the runaway and indicator hypotheses for courtship signal-mediated female choice require that signal magnitude vary among males within the population. This is clearly the case for *Helix* and some other helicids; although the courtship appears stereotyped, there is substantial variability in dart shooting effectiveness and other parameters. This variability has gone unappreciated, perhaps because of the presumed role for the dart in facilitating copulation. In fact, the spectrum of dart shooting effectiveness ranges from none at all to sudden, well-aimed, and forceful dart ejection. Additionally, I have observed many cases of apparent misfirings, including partial and/or premature dart shootings and "self shootings" (a single self-inflicted darting was observed in approx. 150 pairings); these misfirings may represent inferior signals by low-viability individuals. Variability in the quantity and quality of dart mucus produced would contribute further to total signal variability.

(v) Related to this aspect is whether the dart is a "costly" signal. In terms of the materials involved the dart cannot be said to be expensive. The amount of calcium in a dart is equivalent to that in a single egg (Koene & Chase, 1998a), which represents less than 1% of a typical season's production. It is conceivable that the mucus transferred by the dart contains a substance that is costly to produce or acquire, but the composition of the mucus is unknown. However, although there is no evidence that the dart and mucus are materially expensive, dart shooting as a complete behavioral act may be quite costly as

measured in other currencies. The total cost of dart shooting consists of the efficient "presentation" of the signal to the intended receiver. This cost of presentation includes the proximate energetic costs of dart shooting, the genomic/information costs of encoding a properly functioning dart system (revealed through congenital defects in dart system function), and the metabolic/anatomical costs of building and maintaining the dart and mucus delivery system. None of these has been estimated in terms either of energy or fitness units, but the wide variation in dart-shooting ability and the not inconsiderable mass and complexity of the associated organs are consistent with the notion that dart-shooting is a costly signal (Leonard, 1991).

Questions and Further Research

Many of the gaps in our knowledge of the biology of *Helix* are directly relevant to the hypotheses for dart function discussed here. For example, the indicator hypothesis for female choice based on male sexual signals requires a specific relationship between signal magnitude and signaler viability (Grafen, 1990a, Getty, 1998): high-viability males should produce a higher-magnitude signal than low viability males. This question has not been addressed in *Helix*. The answers to a second set of questions, whether greater dart-shooting effectiveness (signal magnitude) results in greater potential or actual paternal reproductive success, have recently been published. Both the amount of sperm stored by mates (Rogers & Chase, 2001) and paternal reproductive success (Landolfi et al., 2001) have been shown to depend on dart shooting effectiveness. However, the indicator, runaway, and male manipulation hypotheses for dart function all predict that better-shooting snails will experience higher levels of sperm storage and paternal reproductive success. Demonstrations of correlations between these parameters will therefore not distinguish among these more ultimate hypotheses for dart function. A third question is that of the bioactive agent in the dart (digitiform gland) mucus. If the mucus is responsible for the differences in allosperm storage and paternal reproductive success, as Koene & Chase's (1998b) study implies, then a study of its composition would be very useful indeed.

Regarding female choice and male manipulation hypotheses for dart shooting, clarification would be aided by the resolution of whether females benefit from receiving courtship, i.e., from dart receipt. The putative fitness benefit would derive from female assessment of the male sexual signal, allowing female choice of mates. If females do derive a fitness benefit from dart receipt, can they be regarded as being "manipulated" by males? On the other hand, the female choice hypotheses would be refuted if it were shown that females suffer a net reproductive fitness decrement while males derive benefits from dart shooting. It nonetheless seems possible that both pro-

cesses, female choice and male manipulation, have interacted to influence the evolution of courtship behaviors and mating systems (Eberhard, 1998). (Manipulation may be more significant in reciprocal hermaphrodites than in gonochorists because the former always participate in courtship simultaneously as both males and females. Selection for increasing male mating opportunities necessarily "exposes" simultaneous hermaphrodites to higher rates of courtship and mating as a female. In contrast, female gonochorists may better optimize costs and benefits of courtship and mating for that sexual mode.)

The theoretical feasibility of the operation of female choice raises a further question: whether this mate choice is sustained by fisherian runaway and/or indicator mechanisms. If signal cost scales with signal magnitude but yet is proportionally lower for high-viability than for low-viability males, it may serve as an indicator of phenotypic viability/genotypic quality. Alternatively, runaway does not specify any consistent relationship between an individual's ability to signal and any of its other qualities (besides its ability to attract mates). Because the runaway and indicator processes likely operate synergistically toward the same end, rendering their distinction by empirical methods has proven to be a challenge.

The resolution of these general issues is central to a full understanding of animal courtship, sexual selection, and the evolution of mating systems.

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